BULLETIN OF MARINE SCIENCE, 53(3): 1099–1116, 1993 CORAL REEF PAPER

SPECIES DISTINCTIONS AMONG SEVERAL CARIBBEAN STONY CORALS

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ABSTRACT

Morphological observations of living corals at Cozumel (Mexico), Martinique, St. Lucia, the Cayman Islands, and Roatan (Honduras) support the view that *Siderastrea radians, Siderastrea siderea, Isophyllastrea rigida, Isophyllia sinuosa, Madracis mirabilis, Madracis decactis, Agaricia lamarcki, Agaricia undata, Mussa angulosa, Mussa cubensis* (=*Scolymia cubensis*), *Millepora alcicornis, Millepora complanata,* and *Millepora squarrosa* represent valid species. However, *Colpophyllia breviserialis* is not supported as a valid species separate from *Colpophyllia natans*; *Madracis pharensis* is supported as a form or ecomorph of *Madracis decactis*; and *Scolymia lacera* is supported as a form or ecomorph of *Mussa angulosa. Madracis mirabilis* f. *martiniquensis* (new form) has flat-ended branches of variable outline and diameter. Calices on the branch ends are deep and cerioid, and some lack a styliform columella, are recessed, and/or lack exsert septa. Living colonies are yellow-brown.

Zlatarski and Estalella (1982) have challenged several of the species distinctions made by the majority of Caribbean coral taxonomists (Squiers, 1958; Duarte-Bello, 1961; Almy and Carrion-Torres, 1963; Roos, 1971; Smith, 1971; Wells, 1973; Wells and Lang, 1973; Tresslar, 1974; Chassaing et al., 1978; Cairns, 1982; Castañares and Soto, 1982; Cortés and Guzmán, 1985; Prahl and Erhard, 1985). Zlatarski and Estalella (1982) collected more extensively than previous workers, allowing intermediates to be discovered. This led them to recognize some corals as forms instead of valid species. Other workers have found evidence supporting the validity of some of these species (Lang, 1971: *Scolymia cubensis* (Milne Edwards and Haime, 1849a), *S. lacera* (Pallas, 1766); Lang, 1973: *S. cubensis, S. lacera, Isophyllastrea rigida* (Dana, 1848), *Isophyllia sinuosa* (Ellis and Solander, 1786), *Mycetophyllia lamarckiana* Milne Edwards and Haime, 1848, *M. aliciae* Wells, 1973, *M. danaana* Milne Edwards and Haime, 1849a, and *M. ferox* Wells, 1973; Stearn and Riding, 1973: *Millepora alcicornis* Linnaeus, 1758, *M. complanata* Lamarck, 1816, *M. squarrosa* Lamarck, 1816; van Moorsel, 1983: *Agaricia humilis* Verrill, 1901; de Weerdt, 1984: *M. alcicornis, M. complanata, M. squarrosa*; Szmant, 1986: *Siderastrea radians* (Pallas, 1766) and *S. siderea* (Ellis and Solander, 1786); de Weerdt, 1990: *M. squarrosa*). Non-skeletal characters were used in four of these studies; a wide variety of such characters may provide a useful supplement to skeletal characters (Lang, 1984). In this study, morphological observations bearing on species validity are reported from nine genera (*Colpophyllia, Madracis, Isophyllastrea, Isophyllia, Siderastrea, Agaricia, Scolymia, Mussa,* and *Millepora*) of living stony corals from Cozumel (Mexico), Martinique, Jamaica, St. Lucia, the Cayman Islands, and Roatan (Honduras).

METHODS

Observations were made at Cozumel (Mexico) in March, June, and July 1988, November 1989, June 1990, and December 1991; at Martinique in March and December 1990; St. Lucia in December 1990 and January 1993; at Roatan (Honduras) in April 1987; the Cayman Islands in January 1988 and June 1989; and Jamaica in February, 1991. For descriptions of research sites see Roberts (1972), Rigby and Roberts (1976), Bouchon and Laborel (1986), Liddell and Ohlhorst (1987), Wells (1988), Fenner (1988, 1991, 1993) and Muckelbauer (1990). Branch dimensions of *Madracis* colonies in Cozumel and Martinique were measured with a ruler and a 2-mm diameter metal rod. The diameter of one branch of average-appearing diameter was measured with the ruler in each colony. The metal

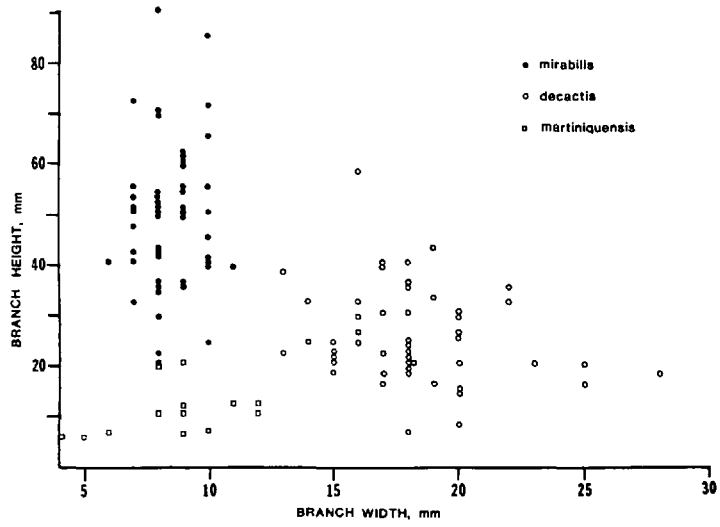

Figure 1. Branch height and width of *Madracis mirabilis, and Madracis decactis* at Cozumel, Mexico, and *Madracis mirabilis* f. *martiniquensis* at Martinique.

rod was inserted between branches as far as possible, marked, removed and measured for branch length.

Observations

Colpophyllia.—Forms intermediate between *Colpophyllia natans* (Houttuyn, 1772) and *Colpophyllia breviserialis* Milne Edwards and Haime, 1849a were observed at the Cayman Islands, Roatan, Martinique, St. Lucia and Cozumel. Of a total of 90 specimens of *Colpophyllia* that were observed at Cozumel, 73 had the typical *C. natans* morphology, with long polycentric valleys. Five specimens had typical *C. breviserialis* morphology, with short, monocentric valleys. Four specimens were bimorphic (Zlatarski and Estalella, 1982), with monocentric and polycentric areas and a sharply defined border between the two areas, but no other signs of colony fusion, such as color differences or differences in sizes or spacing of septa between the two areas. In addition, four bimorphic specimens were observed with a graded transition area between the two extreme areas. Three colonies were judged to have valleys of an intermediate length ('morphological bridge': Zlatarski and Estalella, 1982). One colony was hydnophoroiid, with the collines divided into short sections or cones completely surrounded by valleys (Pfaff, 1969: fig. 2). Two colonies of *Colpophyllia* at St. Lucia were partially hydnophoriid and partially meandroid, without a sharp boundary. Among 50 *Colpophyllia* observed in Martinique, 49 had typical *C. natans* morphology. One colony had intermediate length valleys.

Madracis.—At Cozumel, Jamaica, St. Lucia, Roatan and the Caymans, all *Madracis mirabilis* (Duchassaing and Michelotti, 1860) colonies could be immediately distinguished from *Madracis decactis* (Lyman, 1859) colonies. *Madracis mirabilis* colonies were always a light yellow, with extended polyps, and long, thin branches that often bifurcated. The branches had a circular cross section, with rounded tips. Most colonies were attached, but some colonies were unattached in sand. Only one young *M. mirabilis* colony was partly encrusting. The *M. decactis* colonies that were most similar to *M. mirabilis* were found in well-illuminated

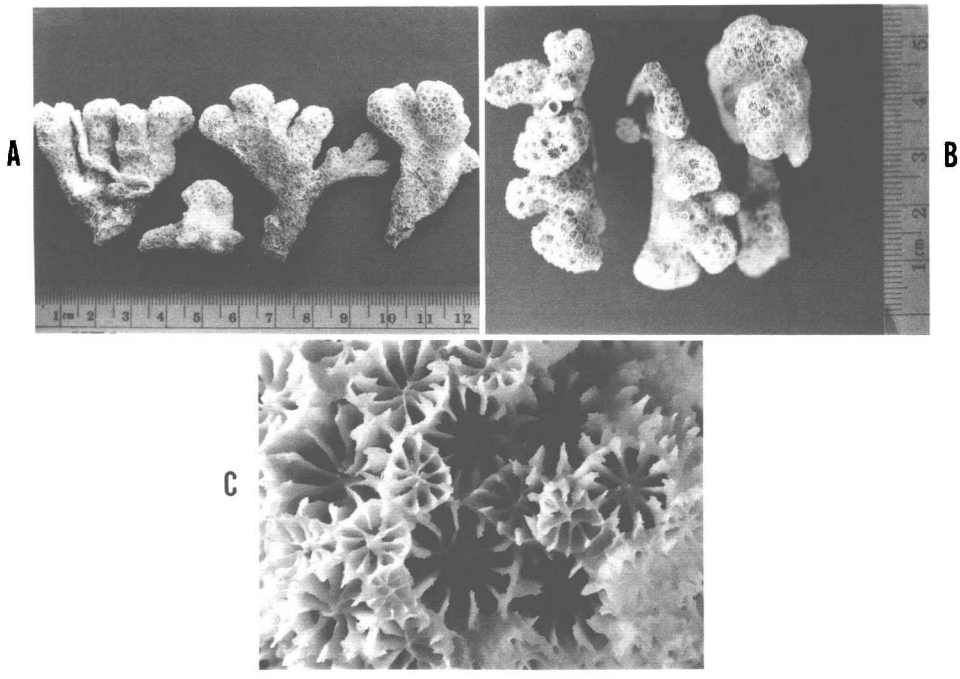

Figure 2. *Madracis mirabilis* f. *martiniquensis*. A. branches, side view. B. view of branch ends. C. terminal calices.

locations, as were all *M. mirabilis*. Well-illuminated *M. decactis* colonies were dark green to yellow-green. All colonies had nodules and/or branches. Most had at least a few branches that were long enough to bifurcate. Larger nodules in each colony usually had oval cross sections, with slightly enlarged tips (clavate). Figure 1 shows the height and width of branches of 50 *M. mirabilis* and 50 *M. decactis* colonies at Dzul-Ha and fringing Pariso reefs in Cozumel. One average-size branch in each colony was measured. *Madracis mirabilis* had longer, thinner branches than *M. decactis,* with no overlap in branch width. There was a range of branch sizes within colonies, particularly in *M. decactis*. Thus, the smallest diameter nodule on an *M. decactis* colony was sometimes thinner than the thickest branch on an *M. mirabilis* colony, even though the average branch diameters did not overlap, and the colonies were easily distinguished by eye.

A total of 305 colonies of *M. mirabilis* and 241 colonies of *M. decactis* in the United States National Museum (USNM) collection were examined, with no intermediates found. This included many specimens collected from the Yucatan by V. Zlatarski.

In Martinique, six short-branched, yellow-brown colonies were seen along with many colonies of *M. mirabilis* and *M. decactis*. The six yellow-brown colonies 10–20 cm in diameter found at 1–3 m depth in the silty water of Fort de France Bay at Anse Mitan have short branches about 0.5–3 cm in length (Pl. 1A, Fig. 2A). The branch tips form a relatively smooth colony surface. Four branches were collected and deposited at the USNM (88830). Branches in these specimens average 10.3 mm in length, ranging from 5–20 mm (N = 13; Fig. 1). Branch diameters are highly variable within each colony, ranging from 4 to 12 mm in the branches collected (average 8.6 mm). Branch tips are clavate with flat ends (Fig. 2A). Branch

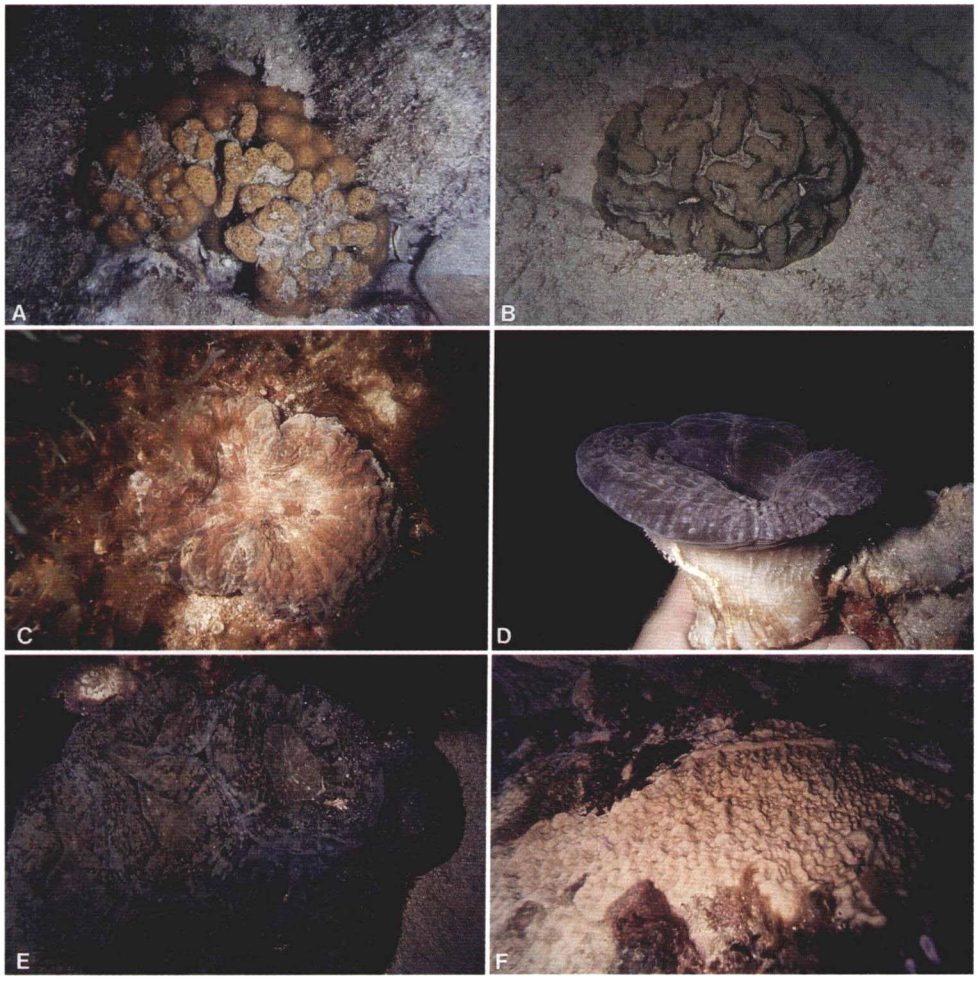

Plate 1. A. *Madracis mirabilis* f. *martiniquensis,* new form. Anse Mitan, Martinique. Polyps are retracted on central branches. B. *Isophyllia sinuosa.* Pariso fringing reef, Cozumel, Mexico. C, D. *Mussa angulosa* f. *lacera.* Cap Salomon, Martinique. E. *Mussa angulosa* f. *angulosa.* Cap Salomon, Martinique. F. *Millepora squarrosa,* rippled colony. Cap Salomon, Martinique.

tips are variable in outline (Pl. 1A; Fig. 2A, B). Branches on the USNM specimens are separated by 1–5 mm, with a mean separation of 2.6 mm (N = 11). Calices on branch ends are 2 mm in diameter, very deep, with the columella consisting only of the intersection of the 10 thin septa (no styliform columella; Fig. 2C). Septa are exsert on some terminal calices, but not exsert on others (Fig. 2C). Terminal calices are cerioid, separated by thin walls, without coenosteum or spines. Some of the calices on the ends of the branches are recessed (Fig. 2B, C). A few calices on the sides of some branches are shallower, have thicker exsert septa, and have a styliform columella. These calices are separated by coenosteum which in some areas bears rows of short spines. In other areas, the coenosteum bears interconnecting sharp ridges (pseudocostae), running parallel or perpendicular to the theca but not as extensions of the septa. Calices on an *M. mirabilis* from Anse Mitan (USNM 91936) are as in the USNM *M. mirabilis* specimens,

except on the end of one branch, where they are similar to terminal calices on the four Anse Mitan branches. However, only one calice lacked a styliform columella and exsert septa. A branch tip (USNM 91937) collected from a typical *M. mirabilis* specimen in a shallow, sandy area (Dzul-Ha) at Cozumel has cerioid calices on the branch tip without exsert septa or styliform columellae. Its terminal calices resemble those of the four Martinique specimens, and the calices on the branch sides are typical of *M. mirabilis*. Near the branch tip, the coenosteum bears pseudocostae.

Other *Madracis* colonies were found in two principal forms, one on cave roofs, and the other outside caves in shady areas. Colonies found on dark cave roofs at depths greater than 20 m appeared to be *Madracis pharensis* forma *pharensis* (Heller, 1868). They were nodular, the nodules about 0.5–3 cm in diameter. Colonies were a cream color, with pink polyps, as shown in Colin (1988: 213 and Humann, 1993: 108, 109). One nodule from Roatan had a second set of 10 small septa (USNM 78505). Many other *Madracis* colonies found outside caves but in shady locations were a variety of colors, and corresponded to *Madracis pharensis* forma *luciphila* Wells, 1973. At Cozumel, dark brown is most common, and bright green second most common. At a depth of about 4 m in Martinique, 27 dark brown colonies were counted, 7 bright green with brown polyps, 6 brown with green mouths, 4 cream with brown tentacles, 2 light green, and 2 greenish brown. Elsewhere in Martinique, a few grey-brown colonies with white tentacles, brown colonies with red tentacles, and dark red-brown colonies were seen. Most colonies were encrusting, forming sheets a few cm to 1 m in diameter, with about 15 cm being most common (Humann, 1993: 106, 107, 109). Some colonies had irregular lumps, up to 5 or more cm in width and height (Humann, 1993: 108). Other colonies had short nodules similar to typical *M. decactis,* but perhaps a bit more irregular, not always close together, and which did not bifurcate. All colonies of all colors were attached. Encrusting colonies were located in less brightly lit areas such as a vertical surface at 5–25 m depth, or the roof of a cave at 3 m depth, within 1 m of the cave entrance. One bright green and four brown colonies were examined in Cozumel with nodules on part of their surface, with the remaining surface encrusting; these two areas were not sharply demarcated. Additional such colonies were seen in both Cozumel and Martinique. Small samples of a smooth brown (USNM 86886) and a smooth bright green colony (86885) at Cozumel each had 10 large septa and 10 small septa per calice. Samples of a lumpy green and lumpy brown colony in Cozumel revealed just 10 septa per calice. Samples of three colonies of different colors in Martinique revealed only 10 septa per calice in each. The height of nodules were measured on 18 well-illuminated green colonies of *M. decactis,* and 48 shaded brown or bright green colonies of *Madracis* in Martinique. A nodule height of 0 was assigned to encrusting colonies. As seen in Figure 3, although a majority of the shaded colonies were encrusting, several had nodules of as great height as some *M. decactis* specimens. One or two colonies in Martinique, and 10 colonies in Cozumel had nodules that appeared identical to those of *M. decactis,* except they were a dark brown and located in the shade on a near-vertical surface. Photos taken with a flash of two of these colonies show the green color typical of colonies in the light. Three colonies were found on the lips of overhangs in Cozumel. The portion of each colony in the sun had the typical green color of an illuminated colony, and the shaded portion of each colony had the brown typical of shaded colonies. It appeared as though the observed color difference may have been due to differences in illumination. In each case, there was a gradual color change between the two areas. In two cases, the entire colony was nodular; the shaded, brown portion of

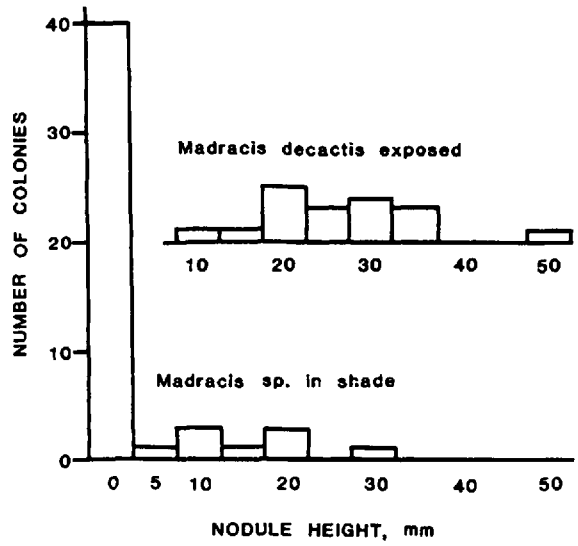

Figure 3. Nodule heights of *Madracis decactis* colonies exposed to sunlight and *Madracis* sp. in shade ("*Madracis pharensis* f. *luciphila*") in Martinique.

one colony was encrusting, and its illuminated area nodular. At depths greater than 25 m, a few brown or bright green lumpy or encrusting specimens could be found in the open alongside *M. decactis* and *M. mirabilis.*

A few colonies of encrusting *Madracis* were found in shallow water in Martinique with most of the colony dark brown, but a small area being cream colored with brown polyps. There was a smooth gradation in color between these areas. One colony found on a vertical surface at about 12 m depth was cream colored with pink polyps. A large clone of encrusting colonies which was found on the roof of a cave entrance at the same depth was dark brown with pink polyps. Most colonies were oval, about 1–3 cm across, and separated from other colonies by 5 mm or less. A few small areas of these colonies were cream colored with pink polyps. A photo of such an area showed a smooth gradation in color from brown to light green to cream. A photo on the top of p. 109 of Humann (1993) shows a large encrusting colony with two small encrusting clones similar to the Martinique clones. Photos of *M. pharensis* on p. 213 of Colin (1988) and p. 108, 109 of Humann (1993) show several greenish areas as well as cream and pink colored areas. A sample from a cream-colored colony of the Martinique clone had shallow calices with 10 septa.

Eleven *Madracis* clones were examined on the roofs of overhangs and caves of Cozumel 22–27 m deep, and eight of these were photographed with flash. Portions of each clone appeared typical of *M. pharensis* f. *pharensis* as shown in Colin (1988) and Humann (1993): white or light pink round or oval nodules 0.5–3 cm diameter with pink polyps, found in dark recesses of cave roofs at about 25-m depth. The nodules were separated by dead areas. Each photo showed that some part of each clone had areas of green or pink between pink polyps. Individual nodules often had areas of different color, with graded coloration between such areas. Clones found deep in shade under overhangs at the same depth appeared mostly brown or green, while clones found in the dark recesses of cave roofs had a larger proportion of white areas. Photos of nodules that appeared to be brown to the unaided eye showed pink nodules. All clones had a wide variety of colony sizes and shapes, ranging from small round nodules to larger, more flattened

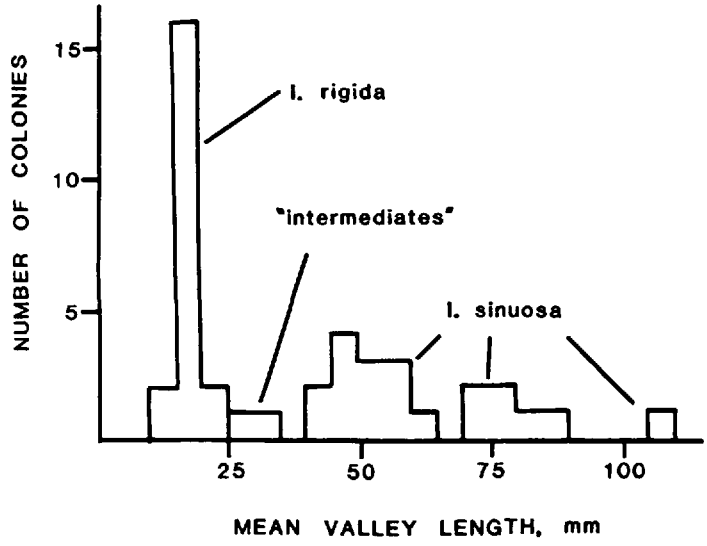

Figure 4. Mean valley lengths of *Isophyllastrea rigida* and *Isophyllia sinuosa* in USNM collection. Two colonies of intermediate appearance are also shown. Means are from 5 valleys in each specimen.

colonies. Samples of a mostly-white clone, and a white nodule of a mostly-brown clone both had more than 10 septa, though a second complete set of 10 was found in only a few calices.

Isophyllastrea *and* Isophyllia.—Colonies of *I. rigida* and *I. sinuosa* were carefully observed at Cozumel's Dzul-Ha and Pariso fringing reefs, and briefly observed at other sites. *Isophyllastrea rigida* had short valleys with one to three centers (usually one), ridges separating the valleys that were usually rough due to spines projecting from the septa, and a dark green-brown color on the ridges and light green on the valley floors (Humann, 1993: 155). *Isophyllia sinuosa* had long meandroid valleys separated by smooth ridges, and a variety of colors, often light green or yellow, which often contrasted between ridges and valleys (Pl. 1B). Ridges often radiated from an indented spot near the center of the colony surface. At fringing Pariso, 774 colonies of *I. rigida* and 63 colonies of *I. sinuosa* were observed; at Dzul-Ha, 67 *I. rigida* were observed. The two species were easily distinguished, with no intermediate colonies of any type found. In causal observations on other Cozumel reefs, many *I. rigida* colonies were seen, but only four *I. sinuosa* were examined, at Paso el Cedral. One of these four *I. sinuosa* colonies was a dark brown, but otherwise identical to the previously observed colonies. In Martinique, three *I. rigida* and four *I. sinuosa* were examined, at St. Lucia 11 *I. rigida* and 31 *I. sinuosa* were examined, and at Jamaica three *I. rigida* and two *I. sinuosa* were examined. All were as described above, except that the *I. rigida* were a little lighter in color, and smoother. No intermediates were seen. A total of 294 *I. sinuosa* and 115 *I. rigida* colonies in the USNM collection were examined. Only two specimens appeared to be intermediates (USNM 74268 and 74275). Valley lengths were measured in five valleys of each of 20 colonies of each species, plus the two intermediate-appearing colonies. Mean valley length was greater in all *I. sinuosa* colonies than in all *I. rigida* colonies (Fig. 4). The mean valley length for *I. sinuosa* colonies was 60 mm, and for *I. rigida* colonies it was 16 mm. The two intermediate colonies had mean valley lengths of 28 and 33 mm, which were indeed intermediate (Fig. 4). Valley lengths were also measured in five valleys of each of 20 colonies of each species at Pariso fringing reef in Cozumel. Two *I.*

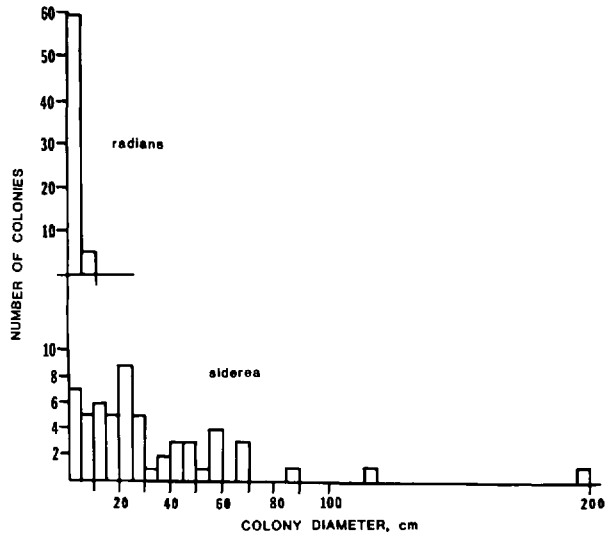

Figure 5. Colony size distributions of *Siderastrea radians* (top) and *Siderastrea siderea* (bottom) at Cozumel, Mexico.

sinuosa were too small to have meaningful valley lengths. Mean valley lengths of all but one *I. sinuosa* were longer than all *I. rigida* mean valley lengths. The one exceptional *I. sinuosa* colony was small, but had the typical appearance of an *I. sinuosa* colony. Valleys in *I. rigida* colonies averaged 11.8 mm long, while in *I. sinuosa* they averaged 37.9 mm long.

Siderastrea.—At each location, living colonies of *S. radians* were found to be white, light tan, or light blue-grey, flat or convex colonies usually less than 10-cm diameter. The center of each calice was a darker tan or blue-grey than the outer edge of the calice (Humann, 1983: pl. 47; Meinkoth, 1981: fig. 16; Humann, 1993: 122, 123). The center of each calice was deeply indented, while the edge of the calice was nearly flat. *Siderastrea radians* was most common on flat coral rock bottoms in water less than 10 cm deep. In contrast, *S. siderea* always had uniform coloration across each calice, with the inner surface of the calices sloping evenly toward the center of the calice (Humann, 1993: 122). Some variation in calice size and shape was noted, but in all cases coloration was uniform, and the identity as *S. siderea* was clear. Hemispherical colonies over 30 cm diameter have the calice morphology of *S. siderea* whether they have brown or bluish-grey coloration (contrary to Colin, 1988: 233), and thus must be *S. siderea.* No bimorphic colonies were found. In Martinique, 33 colonies of *S. siderea* and 137 colonies of *S. radians* were observed without finding any intermediates.

Colonies of *S. radians* and *S. siderea* were observed in Cozumel for calicular morphology and measured for colony diameter. Colonies in only about 10-cm water depth often had some brown tissue coloration over their entire surface more like *S. siderea,* even though they were less than 5-cm diameter, and had narrow, deep calices surrounded by flat colony surface. Close-up photos were taken of five such colonies, allowing the counting of septa. Septa were counted in 7–10 calices of each colony, giving means of 26, 24, 30, 29 and 29 septa. Thus, such colonies were *S. radians* (Cairns, 1982). The photos also showed that most colonies had darker tissue color in the center of the calice than more peripherally. Figure 5 shows size distributions for *S. radians* and *S. siderea. Siderastrea radians* ranged

in size from 1- to 9-cm diameter, with a mean of 2.9 cm. *S. siderea* ranged in size from 1- to 200-cm diameter, with a mean of 33.2 cm. The *S. siderea* distribution contains brown, grey, and intermediate color colonies. The depths of 65 *S. siderea* and 54 *S. radians* were also measured. *Siderastrea radians* was more common in shallow water, and *S. siderea* more common in deep. At 0–2 m depth, *S. radians* represented 96% of *Siderastrea* colonies, while at 3–12 m depth it represented 35%, and at 13–25 m it represented only 13%.

Agaricia.—Observation of *Agaricia* at each location revealed thin, unifacial fronds with distinctive coloration. Most colonies were brown and all had a white star pattern at each polyp. Observation and published color photographs (George and George, 1979: pl. 36/12; Wood, 1983: 89; Newbert, 1984: pl. 48; Sefton and Webster, 1986: fig. 76; Humann, 1993: 138) reveal the white stars to be formed by white mouths surrounded by white tissue over alternate raised septa. In Martinique, a few colonies were greenish brown with white stars, and in St. Lucia one colony was yellow-green with a brown radial section, both with white stars. One small sample taken from a brown colony with white stars in Martinique and one from Cozumel revealed a large, usually oval, styliform columella. Septa alternated in height, with tall septa having sinuous edges and granules on their surfaces. Short septa had smooth sides and straight edges. Tall septa reached nearer to the columella. Septa were much thinner than the interspaces. Thus this was *Agaricia lamarcki* Milne Edwards and Haime, 1851 (Wells, 1973). Examination of the skeletons of whole colonies in Jamaica revealed that in the older areas of the colony, septa were much more nearly equal in height, and much thicker. Very close to the growing edge of the colony, valleys were asymmetrical, with calices closer to the colline nearer the center of the colony.

Living *A. lamarcki* was easily recognized, and no intermediates between it and other agariciids were seen at any location. At Cozumel, 12 colonies of *A. lamarcki* and 408 other colonies of plate agariciids were observed. In Martinique, 75 *A. lamarcki* and 110 other platy agariciids were observed. Over 40 *A. lamarcki* were observed in Jamaica, all brown. A few colonies grew at an angle up from the substrate. Two small samples of a uniformly brown, thin, unifacial agariciid from Cozumel and Martinique had a smaller, round, styliform columella, equal to subequal septa, all with granules on their sides and relatively straight edges. The collines of *A. lamarcki* were smoothly rounded, and smoothly decreased in size toward the end of the colline, before merging with other collines. Adjacent collines were parallel, with few, if any collines at right angles, as can be seen in Cairns (1982: fig. 123e), Zlatarski and Estalella (1982: pl. 124), Humann (1983: pl. 68), Colin (1988: 229) and Humann (1993: 139). Collines in other agariciids usually are sharper, and end by joining with other collines; collines intersecting at right angles are common (Cairns, 1982: fig. 122b–e). Such was the case with all agariciids examined other than *A. lamarcki* and *Agaricia undata* (Ellis and Solander, 1786). Color variations in plate agariciids other than *A. lamarcki* were examined in 76 colonies in Cozumel. Forty colonies were all-brown, 15 were uniformly rust-colored, 14 were brown with green polyp centers (easily distinguished from *Leptoseris cucullata* (Ellis and Solander, 1786) by very different collines), six were entirely dull green, and one was brown with orange mouths. In St. Lucia, one colony was found that was partly green and partly rust-colored, with a sharp color boundary between the two areas. All had sharp collines that intersected at right angles, and were clearly not *A. lamarcki.*

Two *A. undata* were examined at Martinique, and over 50 were examined in Jamaica and St. Lucia, probably representing about 25 clones. All were uniformly

brown, except three colonies in Jamaica which were a light, dull green, and one Jamaican colony that was half brown and half green. Two clones in Jamaica and all in St. Lucia had white edges (Humann, 1983: pl. 66; Humann, 1993: 141, 142, 143). Two clones at 40 m at East Bull, Discovery Bay, Jamaica and all at St. Lucia formed rosettes: concentric rings of colonies projecting upward and outward at about a 45° angle, (Kinzie, 1973: fig. 25; Wells, 1973: fig. 5; Humann, 1983: pl. 66). Collines were long, relatively straight, and paralleled the edge of the colony. On solitary colonies growing over the substrate, the colony was often wedge-shaped (Wells, 1973: fig. 4), with the growing edge on the lower edge. Near the center of the colony, the valleys between collines were V-shaped and symmetrical. Near the edge of the colony, the valleys were flat-bottomed and asymmetrical, with the calices located closer to the colline nearer the center of the colony (Wells, 1973: fig. 4; Chassaing et al., 1978: fig. 23; Humann 1993: 142). No intermediates between *A. undata* and other agariciids were observed at any location. Examination of the skeleton of a wedge-shaped colony at Jamaica revealed the same pattern of collines, valleys, and calices. Septa alternated in height, especially near the edge of the colony and near the columella. Exsert septa had more spines than shorter septa had.

Scolymia *and* Mussa.—About 50 *S. cubensis* were observed at Cozumel. Most were about 1–3 cm in diameter, the largest being 5 cm. The most common color was bright green (Sefton and Webster, 1986: fig. 93), followed by red, brown (Humann, 1993: 157) and grey. One was half green and half red. The oral surface was smooth, with small bumps covering septal teeth. All but one had no more than 1 or 2 mm of flesh on the side of the polyp. One green polyp of 4-cm diameter had 8 mm of flesh, but otherwise appeared like other *S. cubensis.* At Martinique, 26 *S. cubensis* were examined. All were as described for Cozumel, except one 5-cm diameter polyp with 1 cm of flesh at its edge, two 3.5-cm diameter polyps with 5 mm of flesh, and one with 3 mm of flesh. At St. Lucia, 25 were examined: 17 green, 3 brown, 4 with thin alternating radiating brown and green lines, and 1 that was half green and half purple-brown. All had 1 mm of flesh, except three that had 5 mm. In Jamaica, about 40 *S. cubensis* were examined. Included were several that were greyish-purple, four that were bright green with small round white knobs, three that were grey with faint radiating thin orange lines, one red, and one 7-cm diameter coral with a very smooth surface mottled brown and green.

Two *S. lacera* were examined and photographed in Martinique, three in St. Lucia, and two in Jamaica. Each had a rough or verrucose surface (Humann, 1993: 158, 159), and all but two were grey with orange radial lines (Pl. 1B, C). One polyp in Jamaica was light green; one at St. Lucia was mottled green and grey. All were monostomodeal. Two 15-cm diameter circular polyps had 2 cm of flesh on the side of the polyp, which was flush with the sand surface. The fleshy collar was only about 5–10 mm thick vertically (Pl. 1D). A third polyp was oval, 7 by 10 cm. The edge of its polyp was above the substrate, and had only 5 mm of flesh. The fleshy collar appeared to be bent down around the side of the skeleton. The grey individual in Jamaica with orange lines was 6 cm in diameter, and had 15 mm of flesh on the edge, curled down around the polyp. The light green polyp had faint radiating lines of even lighter green. It was 35 × 43 mm in diameter, with 8 mm of flesh bent down around the skeleton.

One *Mussa angulosa* (Pallas, 1766) was examined and photographed at Martinique, 14 at St. Lucia, one at Jamaica, one at Roatan, and four at Cozumel. The polyps of 16 were grey with radial orange lines (Pl. 1E), and had a rough surface. Three were grey without lines (Humann, 1993: 161), one was grey with orange

tones near the center, and one was grey with radiating light grey lines. The edge of each polyp was above the substrate, and the fleshy collar appeared to be bent down around the side of the skeleton. There were about 5 mm of flesh. Polyps ranged from about 5 to 15 cm in diameter. Some were circular and monostomodeal, and others were oval or L-shaped and polystomodeal. The 21 colonies consisted of 2, 3, 4, 6, 8, 12, 14, 15, and about 20, 20, 25, 25, 25, 25, 50, 50, 50, 50, 100 and 200 polyps.

All *Scolymia* in the USNM collection could be assigned to *S. lacera* or *S. cubensis*; no intermediates were found. Four *S. cubensis* were found that had multiple centers on a single calice, and 10 such *S. lacera* were found (including several kept in the *M. angulosa* collection, but otherwise typical of solitary *S. lacera*). *Mussa angulosa* in the USNM collection often had smaller, more concave calices, with thinner septa and longer costa and a longer skeletal column attached than *S. lacera*. However, there appeared to be a complete morphological series joining *S. lacera* and *M. angulosa*.

Millepora.—In Cozumel, hydrocorals of genus *Millepora* were found (Fenner, 1988) with smooth, sharp-edged, intersecting, orange-brown, vertical plates, blades, or paddles arising from encrustations, as described for *M. squarrosa* by Roos (1971: pl. 1) and de Weerdt (1981), and *M. alicornis* f. *squarrosa* by Estalella (pl. 158 in Zlatarski and Estalella, 1982). Intersecting plates usually did not completely enclose spaces. On the upper edge of the junction of plates, small honeycomb formations were sometimes seen, up to 1 cm across. A few colonies had a very small honeycomb pattern on an encrusting area of the colony, with the honeycomb about 1 mm tall, and the spaces about 1 mm wide. Some colonies were found with both intersecting plates and free-standing plates, as found in *M. complanata*.

In addition, smooth orange-brown colonies with thin branches or fingers (*M. alcicornis*) were found. Those in shallow water had (usually unbranching) fingers or branches rising from an encrusting base, while those in deep water usually had branches with little or no encrusting base. Some encrusting colonies had small thick plates with a round base and branches on the top edge of the plate. Some of these colonies also had branches rising from the encrusting base typical of *M. alcicornis* (Tresslar, 1974: pl. 17). Colonies were examined and counted in 0–3 m deep water in front of the Cozumel airport, at Dzul-Ha, and at Barracuda, Galapago, and Villa Blanca Hotels in Cozumel. Colonies with plates and/or intersecting plates numbered 372, including 12 with rounded lumps (Witman, 1988: fig. 2). *M. alcicornis* colonies with branches numbered 159, but no pink colonies covered with large honeycomb and rounded edges, or intermediate colonies, were found. Encrusting colonies without projections were not counted. In Martinique 219 colonies with branches were observed, four with branches on plates, 58 with plates, four with intersecting plates, and one with lumps. Four had plates with a rippled upper edge that appeared intermediate between plates only and plates with fingers (de Weerdt, 1981: pl. 11). At St. Lucia, eight colonies had plates and four had branches. At Jamaica 125 had plates and 66 had branches. Some of the colonies with branches were made of a fan of small plates with branches on their upper edges. Some colonies with very large plates or intersecting plates had rippled upper edges, though these ripples were much shorter than the branches on other colonies.

At Martinique, light pink colonies were found with large honeycomb or boxwork and rounded edges, as shown for *M. squarrosa* in Almy and Carrion-Torres (1963: pl. 3a). Stearn and Riding (1973: fig. 5A), Colin (1988: 140), de Weerdt (1984: pl. 3; 1990: fig. 1) and Humann (1993: 19, 20 (author's photos)). The honeycomb

usually consisted of walls that completely enclosed spaces. Enclosed spaces were typically 1–4 cm in diameter. Colonies were found encrusting rocks in about 2–10 m of water, alongside orange-brown colonies with plates (*M. complanata*) and branching colonies (*M. alcicornis*). Light pink colonies ranged from smooth encrusting, to rippled encrusting (Pl. 1F), to low ridges, to low honeycomb, to high relief honeycomb (Humann, 1993: 19, 20, 21 (author's photos)); honeycomb colonies were the most common. Some small *M. squarrosa* colonies had free-standing plates or intersecting plates not completely enclosing a space. These plates were much thicker than those of *M. complanata,* had a sloping instead of horizontal upper edge, had many small nodules on their sides instead of being smooth, and were pink instead of orange-brown. *M. squarrosa* did not sting me, unlike *M. alcicornis* and *M. complanata. M. squarrosa* could always be quickly identified, and no intermediates between it and other species of *Millepora* were seen. At Martinique, 177 *M. squarrosa* were observed, and at St. Lucia, 468 were observed. Observations on both islands were on their leeward sides. No *M. squarrosa* were observed at Cozumel or Jamaica. These three Caribbean *Millepora* species have different depth ranges. *Millepora complanata* is most common at 0–1 m depth, though it occasionally occurs deeper. *Millepora squarrosa* is most common at about 3–10 m depth. *Millepora alcicornis* is more evenly distributed from 0 m to at least 30 m depth.

Discussion

Morphological observations of *Colpophyllia* colonies at Roatan, the Cayman Islands, Cozumel, and Martinique support the view of Zlatarski and Estalella (1982) and Bouchon and Laborel (1986) that *C. breviserialis* cannot be separated from *C. natans.* Three different types of intermediates were found to be rather common. Although the bimorphic colonies with sharp boundaries between the two areas might have been produced by colony fusion (Hidaka, 1985; Logan, 1988), colony fusion would not have produced bimorphic colonies with a graded boundary, or colonies with intermediate-length valleys. The ability to form colonies with monocentric valleys may be a property of several meandroid species. For example, Roos (1971: fig. 28b) shows a monocentric specimen of *Diploria clivosa* (Ellis and Solander, 1786). Two such colonies of *D. clivosa* were seen in Martinique. Barnes (1973: fig. 9a) shows a specimen of *Diploria strigosa* (Dana, 1848) with small calices containing few centers. In addition, Colin (1988: 286) shows a monocentric colony of *Mycetophyllia ferox.* Such *M. ferox* and a few intermediates have also been seen in Cozumel, the Cayman Islands, and Roatan, (Fenner, unpubl. obs.), and Cuba (Zlatarski, pers. comm.). At least eight species of Indo-Pacific corals each have some meandroid colonies, other colonies that are sub-meandroid with valleys having one, two, or three centers, and other colonies that are combinations of both (Veron et al., 1977; Veron and Pichon, 1980; Veron, 1986).

Madracis colonies were observed which correspond to *M. mirabilis, M. decactis, M. pharensis* f. *pharensis,* and *M. pharensis* f. *luciphila.* No intermediates between *M. mirabilis* and *M. decactis* were found at any location. Intermediates were also not found among the USNM collection. *Madracis mirabilis* and *M. decactis* are found in the same depth range, in sunlight, often next to each other. Their differences are thus most likely not of a genetic, not environmental, origin. The evidence indicates that *M. mirabilis* and *M. decactis* are separate species.

In Martinique, six *Madracis* colonies were found in shallow, turbid water with a distinctive colony morphology. They have short, flat-tipped branches with a diameter similar to that of *M. mirabilis* but a branch length as short or shorter

than that of *M. decactis.* These branches are distinctive from any seen on *M. mirabilis* or *M. decactis* in the field or USNM. The tissue color is a yellow-brown that is closest to that of *M. mirabilis.* The calices on the ends of the branches are not intermediate between *M. mirabilis* and *M. decactis*; rather, those of *M. mirabilis* are intermediate between those of the Martinique colonies and those of *M. decactis.* Zlatarski and Estalella (1982) and Schindler (1985) report that terminal calices are more closely spaced than lateral calices on *M. mirabilis,* and the Cozumel and Martinique *M. mirabilis* branch tips had calices as closely spaced as the Martinique colonies. Terminal calices of the Martinique colonies have several features (e.g., no styliform columella, cerioid calices, septa not exsert on most calices, some calices recessed) which are not found on *M. mirabilis* lateral calices, but were found on Cozumel and Martinique *M. mirabilis* terminal calices. Schindler (1985) found that in *M. mirabilis* (unlike the Martinique colonies), colonies in shallow water had more exsert septa and higher columellae than in deep water. No intermediates in colony shape between the distinctive Martinique colonies and either *M. decactis* or *M. mirabilis* were seen at any island, but similar terminal calices were found on *M. mirabilis* branch tips from Cozumel and Martinique. Thus, these colonies are viewed as a new form or ecomorph of *M. mirabilis*: *M. mirabilis* f. *martiniquensis.*

The color of living coral tissues can be a useful taxonomic character when used in combination with other characters. Most colors in zooxanthellate corals derive from the symbiotic zooxanthellae in their tissues. There are several species and strains of zooxanthellae (Trench and Blank, 1987; Rowan and Powers, 1991) and many color variations which are likely to be genetic variations. Although many coral species display color variations within or between colonies or clones (Hunter, 1985; Chornesky, 1991), color differences between species can also be seen. It is likely that genetic features of the host coral determine the range of symbiont color varieties which can enter into symbiosis with it, making the colony color part of a phenotype corresponding to a particular coral genotype. The different colored strains of zooxanthellae may influence the light regime which a colony can live in, and even influence the growth and shape of the colony.

Madracis decactis, M. pharensis f. *luciphila,* and *M. pharensis* f. *pharensis* lie along a complete morphological bridge or series in colony morphology from clumps of branching nodules to irregularly nodular to encrusting to encrusting clones to nodular clones to azooxanthellate nodular clones. Some colonies were bimorphic, with both encrusting and nodular areas or zooxanthellate and azooxanthellate areas, or a continuous colony and small clones. Although most encrusting colonies were found in shady areas where branching nodular *M. decactis* was uncommon, a few were found alongside *M. decactis* in the open at 25 m. Some encrusting and irregularly nodular specimens had a second set of 10 septa as reported for *M. pharensis* f. *luciphila* by Wells (1973), but others had only 10 septa. Two azooxanthellate clones had more than 10 septa in some calices, and one did not. Zlatarski and Estalella (1982) reported finding a transitional series between calices with 10 septa and those with 20, both between colonies and within colonies. Schindler (1985) found that the number of septa in *M. mirabilis* decreases with depth. Thus, the number of cycles of septa would appear to be an unreliable taxonomic character in these corals. Color was also an unreliable taxonomic character for these corals. Nodular and encrusting colonies displayed a variety of colors in both light and shade. Nodular colonies separated into clones found in caves and on overhangs often had both zooxanthellate and azooxanthellate areas, with graded transitions across living colonies. Several nodular colonies outside caves or on overhangs were seen with cream-colored sections of the colony (including two with pink polyps, like Colin's (1988) and Humann's (1993) photos

of *M. pharensis* f. *pharensis,* and Hubbard and Wells' (1986) report for ahermatypic *M. decactis* in Trinidad).

It is not clear whether the differences in observed color between *Madracis* colonies in different light levels is due to differences in illumination. Some color differences were seen even under the relatively constant illumination of a photographic flash. More likely to be due to zooxanthella strains or species are color differences between similar colonies or parts of colonies in shaded or very dark locations. These corals also seem to be facultative hosts for their zooxanthellae, able to lose their zooxanthellae under low light conditions for at least part of their colony, assuming the appearance of *M. pharensis* f. *pharensis.* Van Moorsel (1988) reports young *Madracis* colonies without zooxanthellae subsequently acquiring zooxanthellae. *Oculina varicosa* Lesueur, 1820, is also a facultative host for zooxanthellae, with zooxanthellae in shallow water but not in deep water (Reed, 1981). *Oculina diffusa* Lamarck, 1816 is a facultative host, with zooxanthellae in sunlight, and without in shaded locations, and some colonies with both conditions on different branches (Humann, 1993: 100, 101). *Astrangia poculata* (Ellis and Solander, 1786) (=*A. danae* =*A. astreiformis*), another facultative host of zooxanthellae, has received more study (Peters et al., 1988). Algal populations in *A. poculata* vary with light intensity. Only zooxanthellate colonies are found in the relatively well-illuminated surface waters of Chesapeake Bay, and azooxanthellate colonies in the poorly illuminated deeper waters. Both are found in a transition zone. Arguments that colonies lacking zooxanthellae might be a different species than colonies having zooxanthellae were judged invalid (Peters et al., 1988). In *Madracis,* the large number and variety of intermediates in colony morphology and color, and the unreliability of the number of septa (Zlatarski and Estalella, 1982), indicate that the three types of *Madracis* colonies should be considered as forms of *M. decactis*: *M. decactis* f. *decactis, M. decactis* f. *luciphila,* and *M. decactis* f. *pharensis.* The fact that these three are most common in three different light regimes and are not commonly found together (unlike *M. decactis* and *M. mirabilis*) supports the view that they are forms or ecomorphs produced by different environments and not genetically different varieties.

Observations of over 900 living *I. rigida* and *I. sinuosa* at Cozumel, Martinique, St. Lucia, and Jamaica supported the view that these two represent valid species, as intermediates could not be found. Lang (1973) found that *I. sinuosa* attacked *I. rigida,* and these two corals had different aggressive responses to eight other species of corals, supporting the validity of *I. rigida* and *I. sinuosa.* Two skeletons of intermediate appearance were found among 409 colonies examined in the USNM collection; it is possible that the living corals would have been readily separable. The rarity of such apparent intermediates (2 out of a total of 1,300 colonies) suggests little or no genetic exchange between these two groups, and thus that they should be considered separate species.

Observations of *Siderastrea* colonies at each site support the view of Wells and Lang (1973) and Szmant (1986) that *S. siderea* and *S. radians* represent separate, valid species. Intermediate calicular morphologies and bimorphic colonies were not observed, and the colony size distributions and depth distributions for the two calice morphologies were quite different. *Agaricia lamarcki* and *A. undata* were also supported as valid species, as intermediates between them and other agariciids were not found at any location.

Scolymia lacera appears distinct from *S. cubensis,* as Lang (1971) and Wells (1971) reported. Most notably, the primary septa of *S. lacera* are thicker and more exsert, teeth are closer together on the septa, the corallum is more often concave, the living tissue is thicker or more fleshy (Lang, 1971), the tissue surface is rougher or more verrucose (Lang, 1971) with several radiating ridges covering

the exsert primary septa, and the living polyp is a light green or grey with radiating orange lines rather than bright green, brown, red, or radiating green and brown lines. Zlatarski and Estalella (1982) report that the skeleton of *S. lacera* differs from *M. angulosa* in that the former is a solitary, monocentric calice, while the later is colonial and polycentric. However, some specimens of most species of *Scolymia* are polycentric (Wells, 1964 and Wood, 1983: *Scolymia vitiensis* Brüggemann, 1877; USNM, this study: *S. lacera* and *S. cubensis*) and/or have budding polyps (Veron and Pichon, 1980: *S. vitiensis, Scolymia australis* (Milne Edwards and Haime, 1849), and *S. lacera*; Logan, 1988: *S. cubensis*). *Scolymia* can exhibit lamellar linkage, or trabecular linkage like *M. angulosa* (Veron and Pichon, 1980; Cairns, 1982). Some *S. lacera* and *M. angulosa* share an unusual color pattern in their living tissue: a grey with pink stripe pattern shown in the Caribbean only rarely by *S. cubensis* (and perhaps never in Indo-Pacific corals: Ditlev, 1980; Randall and Myers, 1983; Wood, 1983; Veron, 1986; Nishihira, 1988; Sheppard and Sheppard, 1991). *Scolymia lacera* and *M. angulosa* do not attack each other with mesenterial filaments, and in fact they have exactly the same aggressive response to all other corals tested, while *S. cubensis* is attacked by *S. lacera,* and has an aggressive reaction to eight corals that differs from that of *S. lacera* and *M. angulosa* (Lang, 1971, 1973). As a result, it is clear that *S. lacera* is more closely related to *M. angulosa* than *M. cubensis.* Among USNM specimens, solitary specimens were often larger, flatter, with thicker septa, shorter costae, and shorter skeletal columns than *M. angulosa,* although there was a complete series between them. There is a complete spectrum of numbers of polyps: one, two, three, four or more. Since the number of polyps increases with age in many corals, multi-polyped individuals may simply be older than single-polyped individuals (Roos, 1964; Wells, 1964). Or it may be that individuals differ in their tendency to divide (which may be genetically controlled). Polystomodeal polyps may be an early stage of intratentacular division, which is why they are common only on multi-polyp colonies. If the single polyps of some individuals continue to grow after they reach a size at which the polyps of multi-polyp individuals divide, one would expect the maximum size of single polyps to be larger than that of polyps in colonies. Thus, a variable tendency for polyps to divide may produce most of the morphological differences between *S. lacera* and *M. angulosa.* Calice shape and septal thickness may be influenced by adjacent polyps and calice size, and the length of the skeletal column by skeletal growth rate and age. The fact that there are some differences between single and multi-polyp individuals, but a continuous series of intermediate individuals indicates that single-polyp *S. lacera* should be considered a form or ecomorph (*M. angulosa* f. *lacera*) of *M. angulosa,* and multiple-polyp colonies considered *M. angulosa* f. *angulosa* (*Mussa* Oken, 1815 has priority over *Scolymia* Haime, 1852). *S. lacera* (Pallas, 1766) is the type species of *Scolymia,* and all other *Scolymia* species (*S. cubensis* (Milne Edwards and Haime, 1849a); *S. wellsi* Laborel, 1967; *S. vitiensis* Brüggemann, 1877; and *S. australis* (Milne Edwards and Haime, 1849)) are congeneric. As a result, *S. cubensis* and other *Scolymia* are also referred to *Mussa. S. wellsi* has the same pattern of septal height and thickness and corallum size as *S. cubensis* (Laborel, 1967; Zlatarski and Estalella, 1982), and the same appearance of the living tissue as *S. cubensis* (Laborel, 1967; Humann, 1993: 157–159). The only distinguishing characteristic is a slight difference in septal teeth. Thus, *S. wellsi* is *Mussa cubensis* f. *wellsi.*

In Cozumel, intermediates between *M. squarrosa* defined as sharp, smooth intersecting plates and *M. complanata* were found, supporting the view (de Weerdt, 1981; Zlatarski and Estalella, 1982) that such *M. squarrosa* is not a valid species. In Martinique and St. Lucia, intermediates were not found between *M. complanata*

and rounded pink honeycomb *M. squarrosa,* supporting the view of Stearn and Riding (1973) and de Weerdt (1984, 1990) that honeycomb *M. squarrosa* is a valid species. When *M. complanata* is defined as having plates and/or intersecting plates, it is largely distinct from *M. alcicornis* as defined as having branches, including branches on the upper edge of small plates. Although a few intermediate colonies were found, they are not common, and it appears that genetic interchange is minimal or nonexistent, supporting Stearn and Riding (1973) and de Weerdt's (1984, 1990) view that they are valid species. De Weerdt (1984) found that these three *Millepora* species could be separated by the size and density of their dactylopores. The presence of *M. squarrosa* at Martinique and St. Lucia but not Cozumel or Jamaica is consistent with de Weerdt's (1990) report that it is found in the eastern but not the western Caribbean. However, the fact that it is common on the leeward sides of islands at depths greater than *M. complanata,* is not consistent with the suggestion (Stearn and Riding, 1973; de Weerdt, 1990) that *M. squarrosa* lives in higher-energy niches than *M. complanata.*

One explanation of the differences between the present findings and those of Zlatarski and Estalella (1982) is that the study of living specimens allows the recognition of several characters in addition to those presented by skeletons alone (Lang, 1984). Some species (e.g., *Euphyllia ancora* Veron and Pichon, 1980 and *E. divisa* Veron and Pichon, 1980; *E. glabrescens* (Chamisso and Eysenhardt, 1821), *E. paraglabrescens* Veron 1990, *E. paradivisa* Veron 1990, and *E. paraancora* Veron 1990; *S. radians* and *S. siderea*) may be distinguished using living specimens, but less distinct or indistinguishable using skeleton alone. Another possible explanation for the differences is that at one site no intermediates between two morphologies may exist, and two species can be distinguished. At another site, the same two morphologies may be connected by a complete series of morphologies, so that the same two species cannot be distinguished. For example, Lang (quoted in Zlatarski and Estalella, 1982: 183) reported that while *Mycetophyllia* species were distinct in Jamaica, they were not distinct in Florida. Similarly, Gattuso et al. (1991) found *Stylophora pistillata* (Esper, 1797) and *S. mordax* (Dana, 1846) to be distinct species in the Gulf of Aqaba, while Veron and Pichon (1976) and Sheppard and Sheppard (1991) were unable to separate them in the Great Barrier Reef and the Red Sea. Due to overlapping study locations, this last example may not prove to depend on differences based on location. However, the present results were consistent over several locations.

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